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THE ARTICULATED CORALLINACEAE (RHODOPHYTA) OF SOUTH AFRICA: 1. *CHEILOSPORUM* (DECAISNE) ZANARDINI

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Abstract

In the first part of this paper *Cheilosporum*, one of the several genera of articulated corallines occurring in South Africa, is examined for the morphological features which have most relevance to the systematics of the genus. Reproductive structures in particular give strong indication that *Cheilosporum* is more closely related to *Jania* and *Haliptylon* than to *Corallina*, *Arthrocardia* and other genera in the subfamily Corallinoideae. Relatively few tetrasporangia develop within a conceptacle, male conceptacles have a characteristic structure that has been seen before only in *Jania* and *Haliptylon*, and the carposporangial conceptacles similarly are like those in these two genera. In the second part of the paper, the taxonomy of the genus is treated. On the basis of examination of hundred of collections, it appears most natural to consider *Cheilosporum* as represented in South Africa by three species: *C. cultratum*, *C. proliferum*, and *C. sagittatum*. *Cheilosporum cultratum* includes two subspecies: *C. cultratum* ssp. *cultratum* and *C. cultratum* ssp. *multifidum* Kützing, comb. nov.

Uittreksel

DIE GEARTIKULEERDE CORALLINACEAE (RHODOPHYTA) VAN SUID-AFRIKA: 1. *CHEILOSPORUM* (DECAISNE) ZANARDINI

In die eerste gedeelte van die artikel word *Cheilosporum*, een van verskeie genera met geartikuleerde korralloïede wat in Suid-Afrika voorkom, ondersoek vir die morfologiese kenmerke wat die meeste betrekking op die systematiek van die geslag het. Voorplantingstrukture gee die beste aanduiding dat *Cheilosporum* nader verwant is aan *Jania* en *Haliptylon* as aan *Corallina*, *Arthrocardia* en ander genera in die subfamilie Corallinoideae. Relatief min tetrasporangia ontwikkel binne 'n instulping, manlike instulpings het 'n kenmerkende struktuur wat voorheen net in *Jania* en *Haliptylon* gesien is en die karposporangiale instulpings is ook soos die van die gemelde twee genera. In die tweede gedeelte van die artikel word die taksonomie van die genus behandel. Nadat honderde versamelings ondersoek is lyk dit logies dat *Cheilosporum* in Suid-Afrika verteenwoordig word deur drie soorte: *C. cultratum*, *C. proliferum* en *C. sagittatum*. *Cheilosporum cultratum* sluit twee subgenera in: *C. cultratum* ssp. *cultratum* en *C. cultratum* ssp. *multifidum* Kützing, comb. nov.

Introduction

The present study reveals salient structural and reproductive features of *Cheilosporum* and provides means for distinguishing the three species of the genus considered to occur in South Africa. *Cheilosporum* is one of six genera of articulated corallines present in this part of the world; the others are *Amphiroa*, *Arthrocardia*, *Corallina*, *Haliptylon* and *Jania*. These genera belong in the Corallinaceae subfamily Corallinoideae, except *Amphiroa* which is included in the

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subfamily Amphiroideae of the same family. The structure, reproduction and systematics of these genera will be treated in subsequent papers.

As currently understood, *Cheilosporum* is a clearly demarcated genus (Johansen, 1969) that appears to bear a closer alliance to *Jania* and *Haliptylon* than to *Corallina* (Johansen, 1970). This possibility needs to be examined, however, because the genus is poorly known, both as to taxonomically important features and as to component species. The study of the species inhabiting South African waters reveals that, in spite of differences in intergenicular shape and conceptacle positions, *Cheilosporum* does indeed belong to the *Jania*/*Haliptylon* alliance. The results of this study also reveal a close anatomical similarity of the South African taxa to *C. jungermannioides* Ruprecht in Areschoug as revealed by Segawa (1941) in the only other detailed study of *Cheilosporum.*

Cheilosporum is represented by three species in the region extending from Mozambique to western South Africa: *C. cultratum* (Harvey) J. Areschoug, *C. proliferum* (Lamouroux) DeToni and *C. sagittatum* (Lamouroux) J. Areschoug. Furthermore, *C. cultratum* includes two subspecies, *C. cultratum* ssp. *cultratum* and *C. cultratum* ssp. *multifidum* (Kützing) comb. nov. (The new combination is formally made later in the text.) The names *Amphiroa cultrata* var. *pectinata* Kützing (1858), *Amphiroa stangeri* Harvey (1847), *Amphiroa flabellata* Harvey (1847), *Amphiroa lamourouxiana* Decaisne (1842b) and *Cheilosporum sagittatum* f. *minor* DeToni (1905) are treated as synonomous with one or the other of the three species which I recognize as occurring in South Africa.

In addition to presenting taxonomic conclusions, another goal of the present paper is to reveal the main anatomical features of the genus. This is based mostly on *C. cultratum*, a common species in South Africa available in all reproductive states.

This paper is the first in a series dealing with the articulated corallines in South Africa. They are based on studies begun in 1967, when I collected extensively in that country. Particularly along the eastern and southern shore of South Africa, articulated corallines often are a common component of shallow waters (Seagrief, 1967), sometimes covering rock surfaces almost to the exclusion of non-corallinaceous algae. In my estimation, this region of Africa rivals or matches central California, parts of Japan and possibly southern Australia (Womersley, Ducker, pers. comm.) in density of corallines and species diversity (see Johansen, 1974).

In articulated corallines, the erect, jointed parts, the fronds, are attached to substrata by holdfasts. The calcified segments are called intergenicula; the uncalcified nodes are genicula.

HISTORY

When *Cheilosporum* was first created as a section of the genus *Amphiroa* (Decaisne, 1942b) based on *Corallina sagittata* Lamouroux (1824) from Mauritius, it was considered as containing articulated corallines with conceptacles located in sharply-pointed intergenicular lobes. The circumscription of the genus has been amplified, and now *Cheilosporum* is regarded as the only genus of the subfamily Corallinoideae which has conceptacles that are solely marginal in origin (Johansen, 1969). Conceptacle initiation occurs in incipient lobes on the margins of terminal or subterminal intergenicula. These lobes usually continue to grow distal to the developing conceptacles and eventually come to protude beyond the deeply embedded chambers. The pore of each mature conceptacle thus is located on the adaxial margin of the lobe (Figs. 5–6).

Seven species that have the characteristics mentioned above have been described on the basis of collections made in South Africa. First, Decaisne (1842b) described *Amphiroa* (Sec. *Cheilosporum*) *lamourouxiana* from plants in Lamouroux's herbarium in Caen. Then, Harvey (1847) described *Amphiroa* (Sec. *Cheilosporum*) *stangeri*, *A.* (*C.*) *flabellata* and *A.* (*C.*) *cultrata*, all from Port Natal (Durban), but the last species stated to occur also at Algoa Bay. In 1858 Kützing described *Amphiroa multifida* from the Cape of Good Hope and *A. heterocladia* from Port Natal, both species having characteristics of *Cheilosporum*. The last, the seventh South African species, *C. africanum*, was described by Manza (1937) from Still Bay, Cape Province, after a lapse of almost 80 years. In addition, since Lamouroux (1824) described *Corallina sagittata* from Mauritius, the type species of *Cheilosporum*, it has been reported to occur also in South Africa (Harvey, 1847, p. 102, as *Amphiroa sagittata*).

MATERIAL AND METHODS

Parts of the thalli to be studied were fixed and decalcified in Susa fixative (Suneson, 1937), usually under decreased pressure. The material was then embedded, sectioned (8 μm) and stained in Ehrlich's haematoxylin in the usual manner.

Most of the specimens examined were collected by: W. E. Isaac, G. F. Papenfuss, M. A. Pocock, R. F. Scagel, S. C. Seagrief, R. H. Simons, various researchers engaged in the Ecological Survey of South Africa from 1932 to 1940 under the leadership of T. A. Stephenson and by myself. These specimens and others are housed in the following herbaria: Albany Museum, Grahamstown, South Africa (GRA); Bolus Herbarium, incorporated into the Department of Botany, University of Cape Town in 1955 (BOL); British Museum (Natural History), London (BM); Clark University, Worcester, Massachusetts (CUW); Department of Botany, University of Cape Town, Rondebosch, where is housed the original set of the Ecological Survey collections (CT); Laboratoire de Botanique, Faculté des Sciences, Caen (CN); Naturhistoriska Riksmuseum, Stockholm (S); personal herbarium of G. F. Papenfuss (GFP), incorporated into the Herbarium of the University of California, Berkeley (UC); personal herbarium of M. A. Pocock (MAP), incorporated in the Herbarium of the Albany Museum, Grahamstown (GRA); Rhodes University, Grahamstown (RUH); Rijksherbarium, Leiden

(L); School of Botany, Trinity College, Dublin (TCD); University of California, Berkeley (UC).

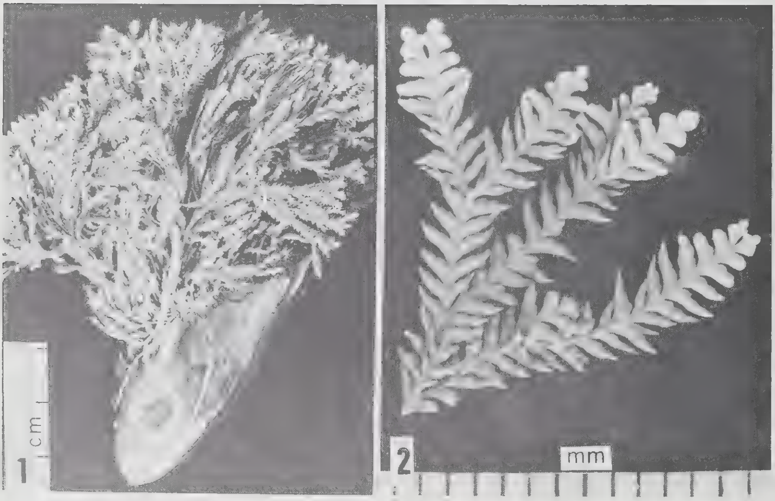
RESULTS

Anatomy

Most of the anatomical and reproductive details presented below were obtained from *Cheilosporum cultratum*. Features whereby *C. sagittatum* or *C. proliferum* differ from *C. cultratum* are pointed out in the systematic part of the paper.

Plants of *Cheilosporum cultratum* as well as of the other species arise in clusters from holdfasts consisting of entangled rhizomatous branches with barrel-shaped intergenicula (Fig. 18). Attachment disks (see Johansen, 1969), which serve to unite holdfasts and secure them to substrata, are present. The plants are usually epilithic, although sometimes they occur on fleshy or calcified algae and mollusc shells (Fig. 1). The development of sporelings and the formation of rhizomes were not studied.

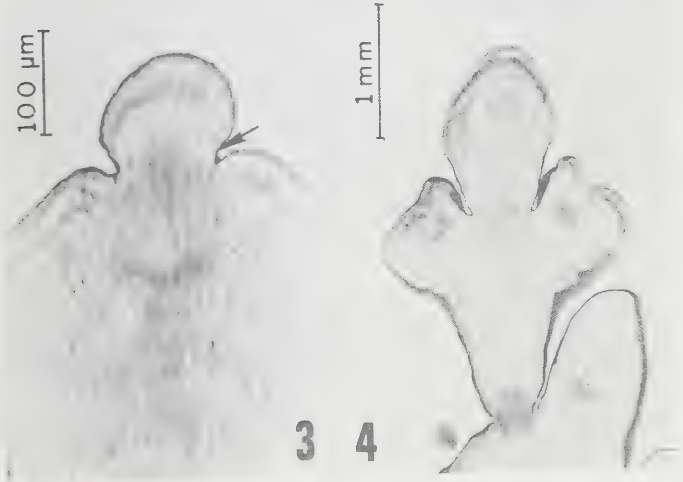
In the lower stipitate parts of the fronds, intergenicula are terete to subterete, about 1 mm long and 1 mm in diameter. Higher in the plant they are flat, up to 2 mm broad and 1 mm long, and each is provided with two characteristic, spreading lobes (Fig. 2).



FIGS. 1–2.
Cheilosporum cultratum ssp. *cultratum*. Fig. 1. Cluster of carposporangial fronds growing on a mussel; Kenton-on-Sea. Fig. 2. Part of a tetrasporangial frond in which most intergenicula bear four conceptacles; Kenton-on-Sea.

Branching is dichotomous. Secondary branches arising from intergenicular surfaces are rare in this species, and when present, they consist of few intergenicula (Figs. 19, 21). In *Cheilosporum proliferum* secondary branches are common and probably account for the specific name. The fronds of *C. cultratum* are usually no more than 6 cm high in tetrasporangial plants and less than that in sexual plants.

A branch consists of a core of achlorophyllous medullary filaments with the cells 90–115 μm long and so arranged that the end walls (and primary pit-connections) form arching, transverse lines in sectioned or decalcified material (Figs. 5, 12). The medulla branches inside each intergeniculum so that a core of filaments extends into each lobe. At intervals of about 1 mm there are tiers of cells only the ends of which are calcified; the uncalcified parts constitute the genicula (Figs. 3–6, 11, 15). These cells may be as much as 425 μm long, but they are only 6–9 μm wide. There is considerable variation in their length, the more peripheral cells being shorter. Genicula are 150–300 μm broad; the dimensions are larger for



Figs. 3–4.

Longitudinal sections through the apices of branches of *Cheilosporum cultratum* ssp. *cultratum*. Fig. 3. Newly formed geniculum and intergeniculum. The bundle of elongate cells (arrow) constitutes the geniculum; the faint spots about midway between the top and bottom are nuclei; Storms River Mouth. Fig. 4. A penultimate intergeniculum each lobe of which contains a young conceptacle primordium. Note also the deeply staining meristematic cells at the branch apex and the two genicula, one between the young conceptacles and another below the fertile intergeniculum, the latter deeply stained; Kenton-on-Sea.

Cheilosporum proliferum. As in other members of the Corallinoideae, flanges, comprised of parts of the adjacent intergenicula, surround the genicula.

All medullary cells are formed by synchronous transverse divisions at the apices of the branches. Branching from peripheral medullary cells in the intergenicular regions (not from genicular cells) results in the formation of cortical filaments that consist of short (up to 15 μm long), plastid-containing cells. Hence, a cortex, 25–40 μm thick in *Cheilosporum cultratum* and *C. sagittatum*, or somewhat thicker (up to 80 μm) in *C. proliferum*, invests the medulla. Surmounting each cortical filament is a cover cell which, when many are taken collectively, comprise a cover cell layer or epithallium. These cover cells are up to 6 μm long and, as in other corallines, have characteristic, peripheral, uncalcified walls which form a more or less continuous cuticle over calcified parts of the plant. All intergenicular cells are 6–10 μm in diameter. They are sometimes joined laterally by large open fusions.

Reproduction

In fertile intergenicula one or two (rarely three) conceptacles form an integral part of each lobe; they are easily recognized by characteristic bulges (Fig. 2). As described earlier, the lobes and conceptacle positions are distinctive of the genus *Cheilosporum* (Figs. 5, 6).

Tetrasporangial conceptacle primordia first appear on the pronounced shoulders of penultimate intergenicula (Figs. 4–5) where they originate at the ends of medullary filaments; they are thus marginal and medullary in origin (see Johansen, 1969). During development the shoulders in which the conceptacles are located grow upward and outward and become lobes.

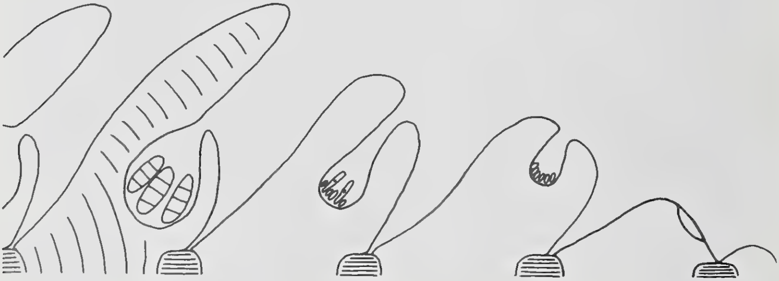
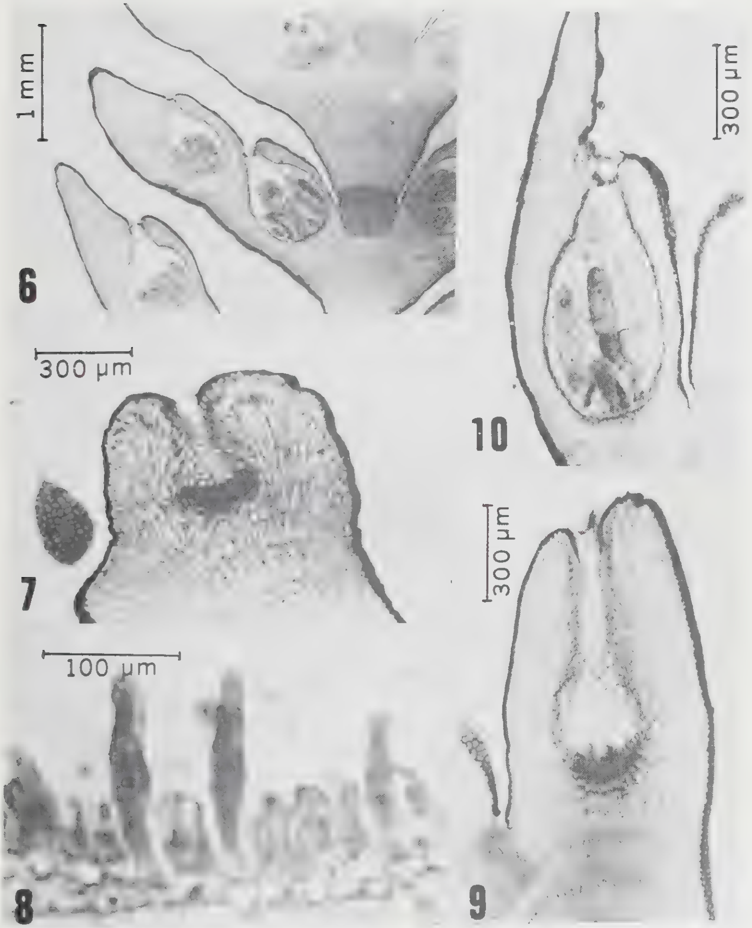


Fig. 5.

Diagram of half of a fertile branch of *Cheilosporum* showing stages in conceptacle maturation and enlargement. The shapes apply most nearly to tetrasporangial and female-carposporangial conceptacles, not to male conceptacles. In one of the lower intergenicula are shown arching lines indicating the lengths of the medullary cells.

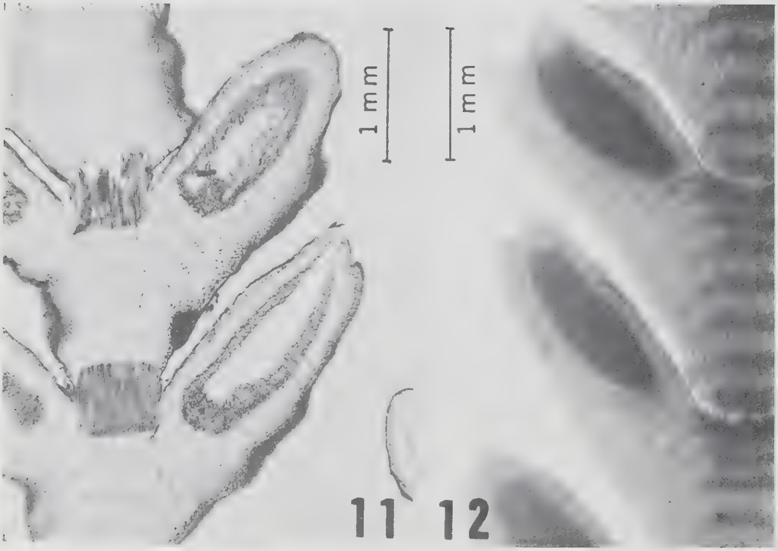


Figs. 6–10.

Sections of tetrasporangial conceptacles of *Cheilosporum cultratum* ssp. *cultratum*. Fig. 6. Part of branch in which there are two mature conceptacles per intergenicular lobe; Kenton-on-Sea. Fig. 7. Conceptacle primordium in which the deeply-stained sporangial initials are surrounded by rapidly growing tissue destined to form the conceptacle roof; Storms River Mouth. Fig. 8. Fertile layer at base of conceptacle in which some of the pre-meiotic tetrasporangia have elongated; Storms River Mouth. Fig. 9. Conceptacle containing pre-meiotic sporangia such as those depicted in Fig. 8. Note geniculum in lower left and the fact that the lobe has elongated unevenly around the fertile area; Storms River Mouth. Fig. 10. Conceptacle containing tetrasporangia; Storms River Mouth.

A tetrasporangial conceptacle primordium consists of a stratum of cells that have differentiated from meristematic cells terminating medullary filaments. These cells are protected by a conceptacle cap of cuticular strata (just as in the female, Fig. 13). Later, usually after the cap is lost, reproductive initials form on the floor of the chamber (Fig. 7). At this time a pronounced development of the tissue surrounding each patch of tetrasporangial initials takes place with the result that the initials come to be located at the base of a deep, narrow cavity (Fig. 9). Growth is asymmetrical with abaxial tissue developing more rapidly than adaxial tissue so that the pore eventually opens on the upper or adaxial surface of the lobe (Fig. 5).

While the surrounding tissues are growing, the tetrasporangial mother cells divide transversely so as to form young tetrasporangia subtended by small stalk cells. At first these sporangia are all approximately the same size, but later certain of them elongate more than their neighbours (Fig. 8). These attain a length of about 100 μm, after which meiosis (presumably) occurs. The four nuclei become evenly spaced on the long axis of the sporangium. Cytokineses are synchronized within each tetrasporangium, and cells undergoing this process are 150 to 200 μm long (Fig. 10). At any one time 10 to 15 post meiotic tetrasporangia may be



Figs. 11–12.
Male conceptacles of *Cheilosporum cultratum* ssp. *cultratum*; Kenton-on-Sea. Fig. 11. A sectioned branch. Fig. 12. A decalcified branch. Note that the conceptacular pores arise on the abaxial surface of the lobes as indicated by the small abaxial processes.

present in a conceptacle; usually numerous small undeveloped tetrasporangia also are present. Bisporangia were never seen in *Cheilosporum.*

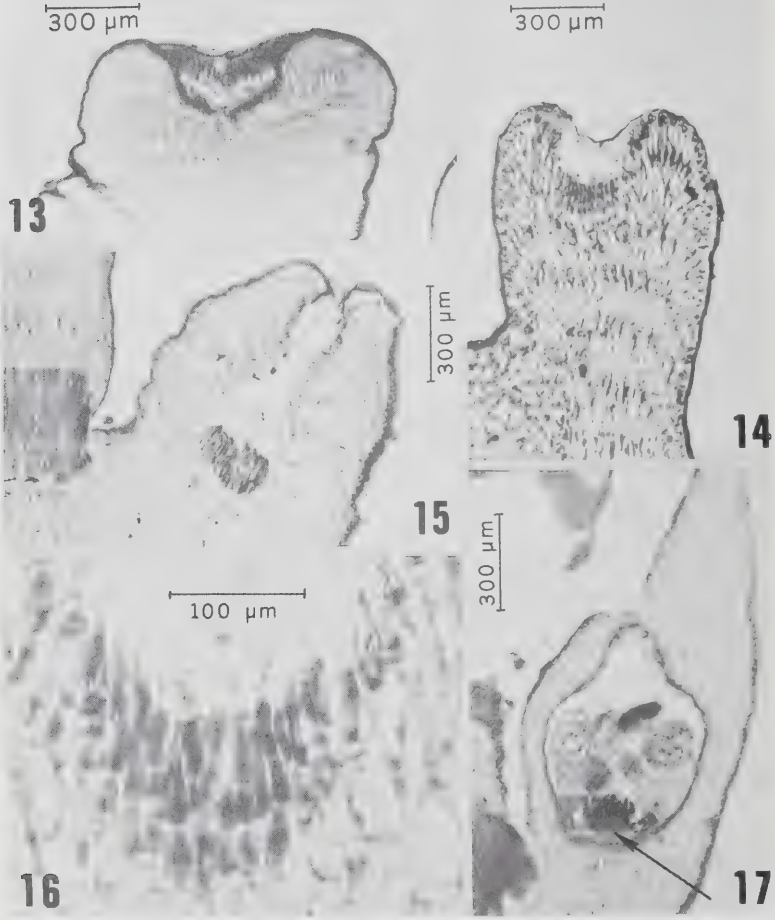
Sexual plants are much less common than tetrasporangial plants. The following description of male conceptacles is based on a few plants collected at Kenton-on-Sea. As in tetrasporangial conceptacles, male conceptacle primordia occur as depressions located on the shoulders of very young intergenicula; in the plants examined, there was never more than one male conceptacle per lobe. As the depression deepens, surrounding filaments continue growing while the filaments at the base of the developing chamber do not. The accentuated development on the abaxial side of the conceptacle observed in tetrasporangial plants is manifested in male plants in a small abaxial spur (Figs. 11–12). Male plants are readily recognized in the field by the fact that the conceptacular swellings are more elongated than in tetrasporangial and carposporangial plants. Also, in a male conceptacle the surface from which reproductive cells (spermatangia) are produced is more extensive, spermatangia occurring on the walls of the chamber as well as on the floor (Fig. 11). Enormous numbers of spermatangia are produced.

The female plants which were studied were collected at Port Alfred and Kenton-on-Sea. Early stages of development are similar to those in tetrasporangial and male plants. As the depression deepens because of circumconceptacular growth, a group of about 150–200 cells terminating filaments at the base become differentiated into intensely staining reproductive initials (Figs. 14–16). They eventually cut off one or two carpogonial filament initials, some of which divide transversely to form 2-celled carpogonial filaments, with the carpogonia bearing long trichogynes. By this time, the female conceptacles are fully formed (Fig. 15) and contain numerous procarps, the more peripheral of which are incompletely developed.

Presumably following fertilization the supporting cells fuse to form a thick, biconvex fusion cell 40 to 70 μm broad and 20 to 30 μm thick (Fig. 17). From the margins of this cell arise the carposporangial filaments, the terminal cells of which become carposporangia 50–70 μm in diameter.

Description of Cheilosporum

Substratum: rock, less often shells or algae; *Holdfasts:* entangled segmented branches consisting of terete or subterete, barrel-shaped intergenicula; *Fronds:* in clumps several centimeters high; *Branching:* dichotomous, secondary proliferous branches sometimes produced; *Intergenicula:* vegetative intergenicula flat, bilobed, lobes projecting distally and diverging much or only a little, lobes often acute, sometimes obtuse; *Genicula:* single cellular tier, cells thick-walled and deeply-staining, ends of cells calcified and embedded in adjacent intergenicula, uncalcified portion of genicula 200–500 μm long; *Medulla:* apical growth occuring at branch tips and, for a limited time, at lobe apices, synchronous divisions and periodic formation of genicula resulting in 5–15 medullary tiers per intergenicu-



Figs. 13–17.

Female and carposporangial conceptacles of *Cheilosporum cultratum* ssp. *cultratum*. Fig. 13. Conceptacle primordium with cap intact; Kenton-on-Sea. Fig. 14. Slightly older conceptacle in which the carpogonial systems have begun to form on the floor of the chamber; Port Alfred. Fig. 15. Older female conceptacle in which there is a hint of trichogynes. Note the geniculum to the left; Port Alfred. Fig. 16. Carpogonial filaments prior to the growth of trichogynes; Port Alfred. Fig. 17. Carposporangial conceptacle. The fusion cell is indicated by the arrow. A gonomoblast filament is emanating from the right side of the fusion cell; Port Alfred.

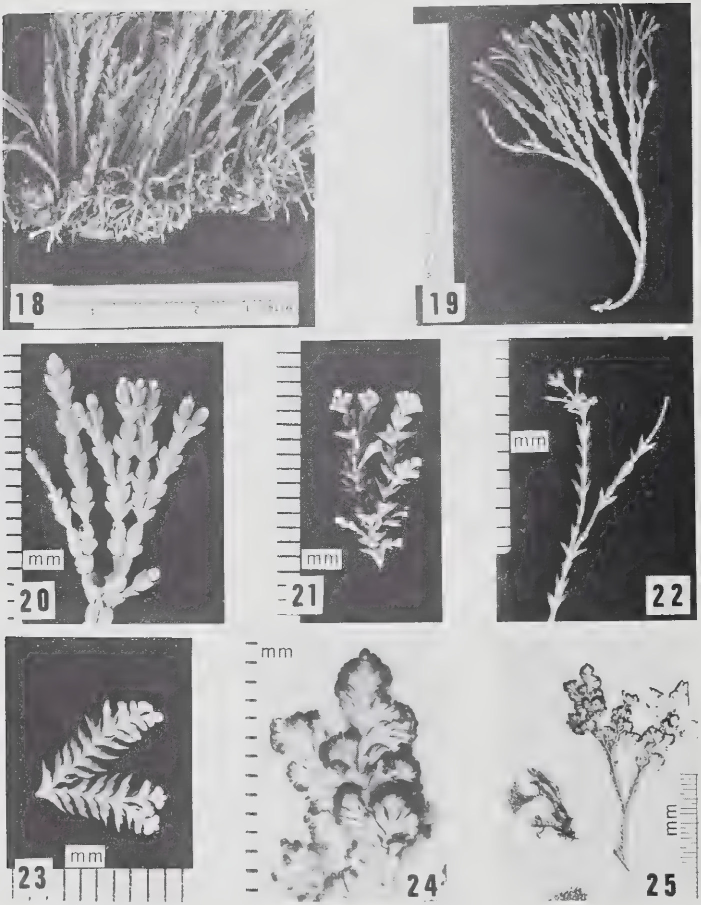
lum, each tier about 80–115 μm high; *Conceptacles:* marginal in origin, one or two (or three) embedded in each lobe of fertile intergeniculum, pore usually on adaxial surface of lobe due to greater growth of abaxial part of lobe; *Tetrasporangial conceptacles:* young conceptacles containing up to 200 tetrasporangial mother cells covering an area less than 150 μm in diameter, in mature conceptacles fewer than 15 tetrasporangia undergoing cytokineses at any one time, tetrasporangia 150–250 μm long; *Sexual plants:* dioecious, usually smaller and more densely bestowed with conceptacles than tetrasporangial plants; *Male conceptacles:* swelling prominently in adaxial part of lobe, chamber 150–250 μm in diameter, canal up to about 120 μm long, fertile surface covering narrow convex floor and high walls of chamber; *Female conceptacles:* chamber about 100 μm in diameter, about 150–200 supporting cells per conceptacle, each bearing 1 or 2 carpogonial filaments; *Carposporangial conceptacles:* chamber 200–260 μm in diameter, fusion cell 20–35 μm thick and 40–70 μm in diameter, with convex upper surface, carposporangial filaments arising from margin of fusion cell, carposporangia 50–70 μm in diameter.

Lectotype species: Cheilosporum sagittatum (Lamouroux) J. Areschoug (Schmitz, 1889, p. 455).

The taxa in Cheilosporum

Features useful in distinguishing among the taxa of *Cheilosporum* in South Africa are shown in Table 1. The characteristics and their variants as used in this table are given below:

1. Lobe Angle (in degrees, see Fig. 26). That angle formed between two lines, one bisecting the intergeniculum along its long axis and the other extending from the midpoint of the lower intergenicular margin to the tip of a lobe.
2. Lobe Complexity.
   sim = Lobes simple.
   inc = Lobes in part broad, flat and incised.
3. Intergenicular Length (in millimeters). As measured along the axis of the upper lobed intergenicula.
4. Medullary Tiers: The number of tiers per intergeniculum.
5. Proliferous Branches: Small branches arising from the intergenicular surfaces in lower parts of fronds:
   rar = Rarely present.
   oft = Often present.
6. Diameter of Stipitate Intergenicula (in millimeters). Referring only to lower intergenicula lacking lobes.



Figs. 18–25.

Photographs of the taxa of *Cheilosporum* treated in this paper. Fig. 18. Basal part of *C. proliferum* showing holdfasts of rhizome-like branches; Injambili River Mouth (Natal Province). Fig. 19. Frond of *C. proliferum* from which several short proliferous branches have arisen; Injambili River Mouth. Fig. 20. *C. proliferum* with a variety of intergenicular shapes; Injambili River Mouth. Fig. 21. A piece of frond from an old plant of *C. proliferum* bearing several adventitious outgrowths; Injambili River Mouth. Fig. 22 *C. sagittatum* in which some of the intergenicula lack lobes. The branch on the left is infected with *Choreonema thurettii*; Southbroom, Natal Province. Fig. 23. *C. cultratum* ssp. *cultratum* in which the intergenicula each contain four conceptacles; Kenton-on-Sea. Fig. 24. *C. cultratum* ssp. *multifidum* showing the characteristic incised lobes and the blackened branch tips; Platboom Bay. Fig. 25. *C. cultratum* ssp. *multifidum*. The lower intergenicula do not have incised lobes; Platboom Bay.

TABLE 1.

Principal features distinguishing the taxa of *Cheilosporum* in South Africa. Characteristics and variants given above.

	1	2	3	4	5	6
C. cultratum ssp. *cultratum*	>60	sim	0,7–1,1	6–10	rar	0,3–0,8
C. cultratum ssp. *multifidum*	>60	inc	0,7–1,1	—	rar	0,3–0,8
C. proliferum	<60	sim	1–2	9–15	oft	0,5–1
C. sagittatum	<60	sim	0,5–1,5	5–8	rar	0,1–0,4

Cheilosporum cultratum (Harvey) J. Areschoug (1852, p. 545) ssp. **cultratum** (Figs. 12, 23, 27). *Amphiroa (Cheilosporum) cultrata* Harvey (1847, p. 102, pl. 39, Figs. 1–3).

Amphiroa cultrata var. *pectinata* Kützing (1858, p. 27, pl. 55, figs. 2g–2i). *Cheilosporum cultratum* var. *pectinata* (Kützing) Yendo (1905, p. 19).

Like the genus but also: fronds up to 60 (–90) mm high; secondary proliferous branches rarely present; branch tips often blackening on drying; intergenicula in holdfasts and lower part of stipe 0,3–0,8 mm long and 0,3–0,8 mm diameter; lobed intergenicula 0,7–1,1 mm long and 1,5–3 mm broad between lobe apices; lobes of vegetative intergenicula usually simple and acute; lobe angles more than 60 degrees (see Fig. 26); 6–10 tiers of medullary cells per intergeniculum.

Type: "Port Natal" (Durban area of South Africa); collected by *Guenzius (TCD!).*

Known distribution in Africa: Southern Mozambique to Platboom Bay near the Cape of Good Hope, South Africa.

REPRESENTATIVE COLLECTIONS EXAMINED

SOUTH AFRICA, specific locality unknown: type of *Amphiroa cultrata* var. *pectinata* Kützing *(L 938,334 . . . 27).*

CAPE PROVINCE: Platboom Bay, male, 19 Dec. 1956, *Pocock 11949* (GRA, CUW); St. James, tetrasporangial, 14 Mar. 1967, *Johansen SA3–180c* (CUW); Riet River, 15 Feb. 1961, *Seagrief 1495 (Pocock 13406)* (RUH); Port Elizabeth, 4 July 1936, *Ecol. Surv. E. 6* (CT); Still Bay, 21 Jan. 1932, *Ecol. Surv. S. 78* (CT); Morgans Bay, carposporangial, 5 Oct. 1951, *Pocock 11757* (GRA); Plettenberg Bay, 10 Feb. 1959, *Isaac B759* (CT); Third Beach, Port St. Johns, 2 Dec. 1962, *Papenfuss and Scagel PR–XLI–56* (UC).

NATAL PROVINCE: Isipingo Beach, *Isaac* (CT); Isipingo, 29 June, 1935, *Ecol. Surv. D. 6* (CT); "Port Natal," *Guenzius (L 939,6 . . . 40)*; "Port Natal," labelled *Amphiroa cultrata* Harvey, *Guenzius* (S); Port Edward, 20 Sept. 1960, *Simons 2204* (CT).

MOZAMBIQUE: Lighthouse Rocks, Cabo Inhaca, Inhaca Island, 26 Sept. 1957, *Pocock 12133* (CUW); 10 Nov. 1962, *Papenfuss and Scagel PR–XXII–135* (UC); Xai-Xai, 10 July 1956, *Isaac B357* (CT); 2–3 Nov. 1962, *Papenfuss and Scagel PR–XIX–106* (UC); Zavora Reef, 4 Nov. 1962, *Papenfuss and Scagel PR–XX–6* (UC).

Cheilosporum cultratum subsp. **multifidum** (Kützing) comb. nov. (Fig. 24, 25, 28). *Amphiroa multifida* Kützing (1858, p. 27, pl. 56, figs. a–b).

Cheilosporum multifidum (Kützing) Manza (1937, p. 571). *Cheilosporum cultratum* f. *multifidum* (Kützing) Yendo (1905, p. 19).

Type: South Africa (''Caput bonae spei''). A specimen sent by *Lappe (L 938,334 . . . 28!).*

Known distribution: Mpekweni, near Hamburg, Cape Province, to Platboom Bay near the Cape of Good Hope. Not reported elsewhere.

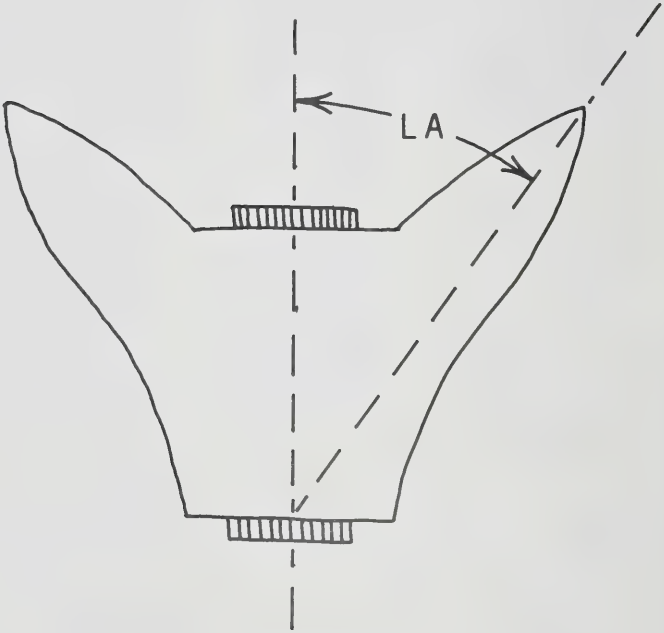


Fig. 26.
Diagram showing how the lobe angle (LA) is determined.

Representative Collections Examined

SOUTH AFRICA, specific locality unknown: *Lappe* (L *939,69 . . . 32).*
CAPE PROVINCE: Platboom Bay, 19 Dec. 1956, *Pocock 11950* (GRA, BOL); Cape Agulhas, 27 Feb. 1937, *Pocock 10915* (GRA), *Papenfuss 74* (UC 564609); Kowie Point, near Port Alfred, tetrasporangial, 15 Apr. 1956, *Pocock 11343* (GRA); Mpekweni, near Hamburg, 19 Jan. 1957, *Pocock* (CUW).

Cheilosporum proliferum (Lamouroux) DeToni (1905, p. 1833). (Figs. 18–21, 30–34). *Corallina prolifera* Lamouroux (1816, p. 291, pl. 10, fig. 5).

Arthrocardia prolifera (Lamouroux) Descaisne (1842a, p. 359). *Amphiroa (Arthrocardia) prolifera* (Lamouroux) Descaisne (1842b, p. 125). *Amphiroa (Cheilosporum) stangeri* Harvey (1847, p. 101, pl. 39, fig. 1–3). *Cheilosporum stangeri* (Harvey) Areschoug (1852, p. 544). *Amphiroa (Cheilosporum) flabellata* Harvey (1847, p. 101, pl. 39, figs. 1–4). *Amphiroa heterocladia* Kützing (1858, p. 28, pl. 58, figs. f–h).

Like the genus but also: fronds up to 100 mm high; short secondary proliferous branches containing fertile intergenicula common; intergenicula in holdfasts and lower part of stipe 0,5–2 mm long and 0,5–1 mm diameter; lobed intergenicula 1–2 mm long and up to 3,5 (–6) mm broad between lobe apices; lobes of vegetative intergenicula acute or obtuse; lobe angles less than 60 degrees (see Fig. 26); fertile intergenicula in main branches usually smaller than vegetative ones; fertile intergenicula near branch tips or in proliferations usually very much smaller, about 1,5 mm long and 1,5 mm broad between lobe apices; 9–15 tiers of medullary cells per intergeniculum.

Type: Madascar (“Indes Orientales,” see Papenfuss, 1952, p. 169) sent by *Jussieu* (CN!).

Known distribution in Africa: Northern Mozambique to Still Bay, Cape Province.

Representative Collections Examined

CAPE PROVINCE: Still Bay, type of *Cheilosporum africanum* Manza, 26 Jan. 1932, *Ecol. Surv. S.80* (UC *564605*; isotypes in UC *564604* and CT); Storms River Mouth, tetrasporangial, in drift, 9 May 1967, *Johansen SA5–223* (CUW); Lighthouse Beach, Port Elizabeth, in drift, 10 Dec. 1962, *Papenfuss and Scagel PR–XLIX–B–26* (UC); Bashee River Mouth, 27 Sept. 1939, *Pocock 1766* (GRA).
NATAL PROVINCE: “Port Natal,” type of *Amphiroa stangeri* Harvey, *Guenzius* (TCD!; isotypes in BM! and S!; “Port Natal” labelled *Amphiroa heterocladia* Kützing, *Guenzius* (S!); “Port Natal” type of *Amphiroa flabellata* Harvey, *Guenzius* (TCD!); Port Edward, 30 Nov. 1962, *Papenfuss and Scagel PR–XXXVIII–94* (UC); Isipingo, 29 June 1935, *Ecol. Surv. D.6* (CT); Reunion Rocks 27 Nov. 1962, *Papenfuss and Scagel PR–XXXIV–89* (UC); Chakas Rocks, 14 Oct. 1951, *Pocock 11743* (GRA).

MOZAMBIQUE: Xai–Xai, 2 and 3 Nov. 1962, *Papenfuss and Scagel PR–XIX–109* (UC).

Cheilosporum sagittatum (Lamouroux) J. Areschoug (1852, p. 545) (Figs. 22, 29). *Corallina sagittata* Lamouroux (1824, p. 625, pl. 95, figs. 11–12). *Arthrocardia sagittata* (Lamouroux) Decaisne (1842a, p. 359). *Amphiroa (Cheilosporum) sagittata* (Lamouroux) Decaisne (1842b, p. 125). *Cheilosporum sagittatum* f. *minor* DeToni (1905, p. 1832). *Amphiroa lamourouxiana* Decaisne (1842b, p. 125).

Like the genus but also: fronds up to 70–100 mm high; secondary proliferous branches rarely present; intergenicula in holdfasts and lower part of stipe 0,3–0,7 mm long and 0,1–0,4 mm diameter; lobed intergenicula 0,5–1,5 mm long and 1–1,5 (–1,8) broad between lobe apices; lobes of vegetative intergenicula usually simple and acute; lobe angles less than 60 degrees (see Fig. 26); 5–8 tiers of medullary cells per intergeniculum.

Type: Mauritius (''sur les rochers de l'Ile-de-France'') (CN!).

Known distribution in South Africa: St. Lucia Bay, Natal Province to Melkbosch, Cape Province.

Representative Collections Examined

SOUTH AFRICA, specific locality unknown: type of *Amphiroa lamourouxiana* Decaisne, *Carmichael* (CN!).
CAPE PROVINCE: Melkbosch, in drift, 12 May 1967, *Johansen SA3–173d* (CUW); Storms River Mouth, tetrasporangial, 9 May 1967, *Johansen SA5–214* (CUW); Hamburg, 3 Dec. 1956, *Pocock 11884* (GRA); Port St. Johns, 7 July 1959, *Isaac B869* (in part) (CT); Fossil Head, 1 Dec. 1962, *Papenfuss and Scagel PR–XL–85* (UC).
NATAL PROVINCE: Trafalgar Port O'Call, in drift, 30 Nov. 1962, *Papenfuss and Scagel PR–XXXIX–80* (UC); Southbroom, 23 May 1967, *Johansen SA5–268* (CUW).

Discussion

Studies of the *Jania/Haliptylon/Cheilosporum* complex have been few and most of our information is based on work on *Jania rubens* (L.) Lamour. (Suneson, 1937), *Jania radiata* Yendo (Segawa, 1946), *Jania iyengarii* Ganesan (Ganesan, 1965) and *Haliptylon subulata* (Ellis & Soland.) Johans. (Johansen, 1970) as well as the only other species of *Cheilosporum* to have been examined closely, *C. jungermannioides* (Rupr.) J. Aresch. (Segawa, 1941). From these and other works as well as the present study, it is clear that the distinctive genus *Cheilosporum* is closely related to *Jania* and *Haliptylon* although it is markedly different as far as conceptacle position is concerned. In *Jania* and *Haliptylon* conceptacles are axial in origin (Johansen, 1969, 1970), that is, the primordia (and the resulting conceptacles) are in line with the genicula subtending the fertile intergenicula.

Hence, an intergeniculum bears only one conceptacle, because the primordium usurps the space in line with the subtending geniculum. On the other hand, as described earlier in the present paper, the conceptacles are marginal in *Cheilosporum* and not in line with subtending genicula. Two or more conceptacles may thus be borne on a single intergeniculum, usually one in each of the two lobes.

Another result of having axial conceptacles is that the extension by growth of the axis of the branch is interrupted. In *Jania* and *Haliptylon* most fertile intergenicula bear two branches, but they are not in line with the axis of that intergeniculum. In *Cheilosporum* fertile intergenicula are intercalary in long branches that only periodically branch dichotomously. Therefore, fertile intergenicula do not interfere with branch systems.

Cheilosporum probably evolved from ancestors such as *Jania* or *Haliptylon* with the most distinctive feature separating it from these genera being conceptacles position. In fact, among the other aspects examined, no differences from *Jania* and *Haliptylon* were observed and the *Jania*/*Haliptylon* alliance can be considered to also include *Cheilosporum*.

It may prove useful to compare this three–member alliance with the remaining nine genera in the subfamily. The comparable differences are given in Table 2 in which *Corallina* represents these genera. Notably, *Corallina* exhibits features which are for the most part coarser than those in the alliance. The fact that most of these features are disjunct suggests that evolutionary routes resulting in these two groups of genera diverged a long time ago. These conclusions are supported by conceptacle morphology (see also Johansen, 1970, 1972).

TABLE 2.

The salient differences between *Cheilosporum* and its two close relatives *Jania* and *Haliptylon* on the one hand and *Corallina* on the other. This table is an updating and amplification of Table 1 (p. 84) in Johansen (1970).

CHARACTERISTICS	CHEILOSPORUM, etc.	CORALLINA
Height of intergenicular medullary tiers (μm)	80–170	50–90
Diameter of fertile area in conceptacles containing tetrasporangial initials (μm)	60–150	150–250
No. of tetrasporangial initials per conceptacle	<200	>200
No. of tetrasporangia undergoing cytokineses per conceptacle	5–15	30–40
Length of conceptacular canal in male conceptacles (μm)	<120	>200
Diameter of fertile area in female conceptacles prior to fertilization (μm)	60–120	150–200
No. of supporting cells per female conceptacle	<200	>200
Diameter of fusion cell (μm)	40–70	90–200

The principal characteristics used in distinguishing the three South African species of *Cheilosporum* are segment size, lobe shape, and the configuration of lobes in relation to the body of the intergeniculum. In spite of considerable variation in intergenicular size in non-stipitate parts of *C. proliferum*, the consistently larger and thicker segments of stipes and holdfast immediately set this species apart from the other two. In the upper part the lobes are either obtuse or acute in *C. proliferum* but nearly always acute in *C. sagittatum* and *C. cultratum*. The separation of *C. sagittatum* and *C. cultratum* is best carried out by comparing their so-called lobe angles in vegetative intergenicula in upper parts of the fronds. This angle is that formed between the intergenicular axis and a line connecting the lowermost point on that axis and one of the lobe apices (Fig. 26). This procedure accentuates the differences between the species because it takes into account the length of the lobe, the distance its apex is from the axis of the branch, and the length of the intergeniculum. The lobe angle is appreciably more acute in *C. sagittatum* than in *C. cultratum*.

Cheilosporum cultratum ssp. *cultratum* is characterized by plants with short intergenicula having relatively narrow and acute lobes that diverge widely from the branch axis (Fig. 2). In Natal Province the fronds are generally smaller and more delicate and, except for the lobe angles, some plants could be confused with those of *C. sagittatum*. Generally, plants of *C. cultratum* ssp. *cultratum* in Natal Province and northwards have a lower proportion of fertile to sterile intergenicula than do plants in the Cape Province. The area between East London and Cape Point harbours plants which are heavily beset with conceptacles, having one to three (usually one or two) conceptacles per lobe, with most upper intergenicula fertile. This subspecies occurs at least as far north as Xai-Xai, Mozambique, a village about 10 miles northeast of the mouth of the Limpopo River (Isaac, 1957). Its relationship to *Cheilosporum jungermannioides*, which has been reported from Kenya (Isaac, 1971), is unclear.

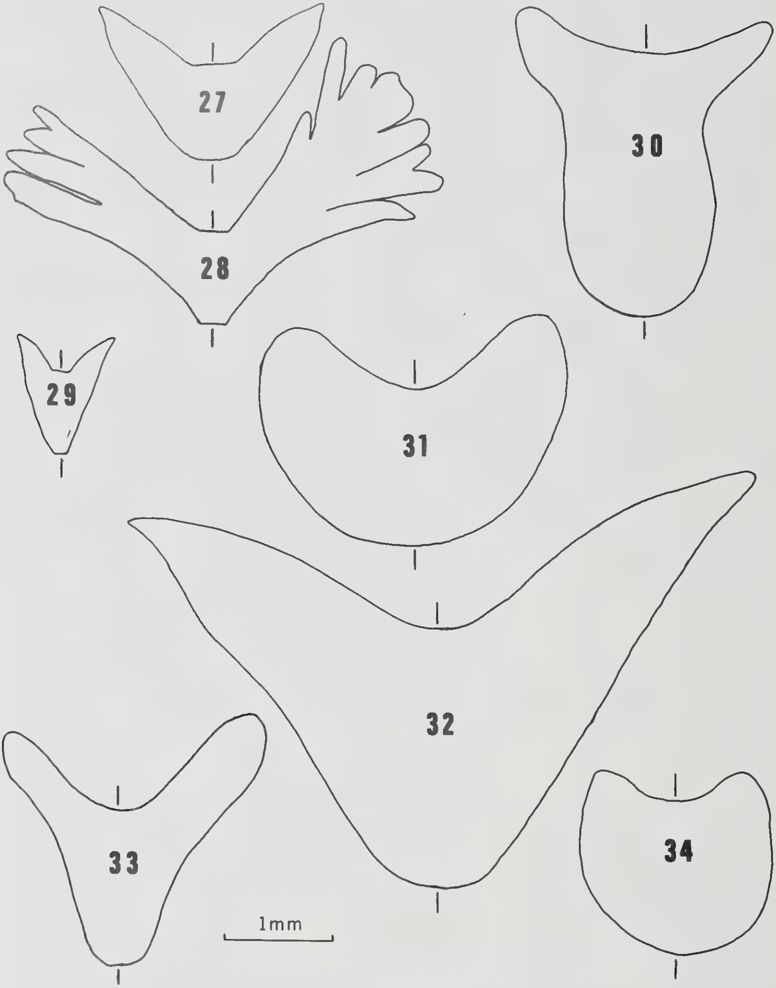
That *Cheilosporum cultratum* ssp. *cultratum* is characterized by plants of variable shape is evidenced by Kützing's (1858) separation of it (as *Amphiroa cultrata*) into three variaties; namely, *debilis, globulifera*, and *pectinata* (the first two *nomina nuda*), all of which were based on plants from South Africa. (It should be noted, however, that the variety *globulifera* was so named because of the ". . . eigenthümliche Kugeln . . ." (p. 27) which, in Kützing's figure (pl. 55, fig. I), may be seen to be conceptacles of the parasitic *Choreonema)*. Harvey (1847, p. 102) mentioned the three varieties but stated ". . . appearances probably caused by locality. In all, the form of the articulations is very similar." He considered them to represent forms of a single species. Furthermore, my placement in *C. cultratum* of what has often been considered a distinct species, *C. multifidum*, underscores the variation in form which thalli of this species possess. The presence of intergenicula characteristic of *C. cultratum* ssp. *cultratum* in parts of plants of *C. cultratum* ssp. *multifidum* makes the separation of the two as discrete species unrealistic. Plants of the latter are rare and usually have few, if any, conceptacles.

In South Africa plants of *Cheilosporum cultratum* ssp. *cultratum* and *C. sagittatum* may, in most instances, be easily distinguished in the field. In addition to intergenicular shape, South African specimens may be distinguished by the purple colour of the former and the red-pink colour of the latter. Furthermore, the tips of the fronds of both subspecies of *C. cultratum* often blacken upon drying (Fig. 24–25; see also the water-colour painting in Seagrief, 1967, p. 127); this does not occur in *C. sagittatum. Cheilosporum cultratum* ssp. *cultratum* is more abundant in intertidal tide pools than is *C. sagittatum*, often forming soft tufts on mussels or rocks.

Cheilosporum proliferum has intergenicula which are, for the most part, longer, broader, and thicker than those of *C. cultratum* and *C. sagittatum*. Therefore, intergenicular size, and especially the more consistently larger segments of the rhizomes and lower stipe, enable one to readily identify this species. In this species particularly, intergenicula in upper parts of the fronds are extremely variable in both size and shape. The factors that account for this great variability are not clear, but probably involved are frond age, the season in which the intergenicula were produced, localities in which the plants grew (with all attendant factors), and the proportions of the fronds given over to bearing conceptacles.

Plants of *Cheilosporum proliferum* change considerably in aspect as the fronds grow in length. Young fronds less than 5 cm long are sterile and usually have subterete to compressed, thick, and more or less round-lobed intergenicula (Figs. 30–31, 34). Subsequent growth may result in dichotomously branched fertile fronds in which conceptacles are present in some of the intergenicula near branch ends. When lobes are given over to bearing conceptacles, they do not develop to the extent as the sterile lobes. Also, the apices of fertile lobes are nearly always acutely pointed, whereas sterile lobes are often subacute or obtuse. Whether fertile or not, intergenicular size usually decreases at each dichotomy and branch ends may consist of short segments only 1–1,5 mm broad between lobe apices. Finally, the tendency for crops of secondary proliferous branches to be produced in older plants is more pronounced in this species than in the other two species of *Cheilosporum*. Usually, the secondary branches issue from flat surfaces of intergenicula in various parts of the fronds and reach a length of less than 20 mm. Most secondary branches are fertile and have small intergenicula (Fig. 21) in which most of each lobe consists of a conceptacle. Most, if not all, members of the Corallinoideae have this ability to produce secondary branches, but *C. proliferum* is often especially proliferous and a specimen of this nature apparently inspired the epithet. The extent to which the other factors mentioned above may help to account for variation in intergenicular morphology is unclear.

As shown in Figures 30–34, vegetative intergenicula may be variously shaped. The most frequently encountered shape has simple spreading acute lobes (Fig. 32).



Figs. 27–34.
Traced outlines of intergenicula in the species of *Cheilosporum* treated in this paper. Fig. 27. *C. cultratum* ssp. *cultratum*; St. James. Fig. 28. *C. cultratum* ssp. *multifidum*; Port Alfred. Fig. 29. *C. sagittatum*; Hamburg. Figs. 30–34. *C. proliferum*. Figs. 30, 31 and 33 from Storms River Mouth (drift); 34 from Injambili River Mouth; 32 from Still Bay (from type specimen of *C. africanum*).

Broadly rounded lobes (Fig. 31), spreading lobes issuing from only the upper part of the segment (Fig. 30), and rounded lobes appressed towards the intergenicular axis (Fig. 34) are less frequent. All of these types, as well as intergradations, may occur in one and the same frond and are not worthy of taxonomic recognition. Two or more intergenicular types may alternate with some regularity in a given branch or one type may predominate for a length of several segments only to be replaced higher in the frond by another type. Harvey's illustrations (1847, pl. 39) of two of his species, *Amphiroa (Cheilosporum) stangeri* and *A. (C.) flabellata*, also show these segment shapes.

It is noteworthy that *Cheilosporum* and *Jania* are abundantly represented by species of large plants (i.e. *Jania crassa* Lamouroux and *C. proliferum*) in the relatively warmer waters of Natal Province, whereas the general tendency in other genera (including non-corallinaceous genera) is for the smaller or more delicate species to predominate in warmer waters and the more robust species to occur in colder waters. To judge from Harvey's (1847) work, Dr. Pocock's collections, and personal field work, *C. proliferum* is the most abundant species of this genus in Natal Province, at least in the intertidal zone. *Cheilosporum proliferum* is present only in the subtidal zone on the southern coast of South Africa.

The varied appearance of intergenicula and branches in *Cheilosporum proliferum* has led to the description of several species based on collections of this taxon made in South Africa. In 1847 Harvey, without mentioning *Corallina prolifera* Lamouroux, the binomial upon which *Cheilosporum proliferum* is based, erected *Amphiroa (Cheilosporum) stangeri* and *A. (C.) flabellata* from "Port Natal". An examination of the types of these species reveals plants that fall well within the circumscription of *C. proliferum*, as do also the types of *Amphiroa heterocladia* Kützing (1858) from Port Natal and *Cheilosporum africanum* Manza (1937) from Still Bay, Cape Province. Plate 58 of Kützing's work illustrates branches of Harvey's two species as well as of *A. heterocladia* and gives a further idea of the kinds of intergenicula present in *C. proliferum*.

To judge from previous reliable references to *Cheilosporum sagittatum* (e.g., Segawa, 1941; Joly, 1965, p. 137; Taylor, 1960, p. 408), it is evident that this species is widespread in tropical areas of the northern hemisphere as well as in the southern hemisphere. The main characteristic of this species is the sharply upswept, acute intergenicular lobes. The type specimen of this species is a relatively robust plant from Mauritius (Ile-de-France); most of the South African specimens are more delicate.

As in many other algae, plants of *Cheilosporum sagittatum* occurring in the sublittoral zone tend to be more spindly and laxly branched than those growing in the littoral zone (Johansen and Colthart, 1975). Also, specimens from Natal Province sometimes have more delicate intergenicula than those from cooler waters, although this may not always be true. This species is less frequently collected in the Cape Province than is *C. cultratum*, possibly because *C. sagitta-*

tum is generally restricted to the subtidal zone. Also, fertile specimens of *C. sagittatum* are less frequently encountered than are sterile specimens.

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